Response of seedlings of different tree species to elevated CO_2 in Changbai Mountain

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Abstract: Eco-physiological responses of seedlings of eight species, *Pinus koraiensis, Picea koraiensis, Larix olgensis, Populus ussuriensis, Betula platyphylla, Tilia amurensis, Traxinus mandshurica* and *Acer mono* from broadleaved/Korean pine forest, to elevated CO_2 were studied by using open-top chambers under natural sunlight in Changbai Mountain, China in two growing seasons (1998-1999). Two concentrations of CO_2 were designed: elevated CO_2 (700 μmol·mol^{-1}) and ambient CO_2 (400 μmol·mol^{-1}). The study results showed that the height growth of the tree seedlings grown at elevated CO_2 increased by about 10%-40% compared to those grown at ambient CO_2. And the water using efficiency of seedlings also followed the same tendency. However, the responses of seedlings in transpiration and chlorophyll content to elevated CO_2 varied with tree species. The broad-leaf tree species were more sensitive to the elevated CO_2 than conifer tree species. All seedlings showed a photosynthetic acclimation to long-term elevated CO_2.

Keywords: Elevated CO_2; Eco-physiological response; Changbai Mountain
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Introduction

Before the industrial revolution, CO_2 concentration in atmosphere was about 265 μmol·mol^{-1}, after then it dramatically increased to 314 μmol·mol^{-1} in 1960s and353 μmol·mol^{-1} in 1990s. Now the mean CO_2 concentration is increased by 1.8 μmol·mol^{-1} annually (Houghton *et al.* 1996; Sanders *et al.*1991). This is due to the increasing consumption of fossil fuel and other human activities. If this momentum continues, the atmospheric CO_2 concentration would be doubled by 2030 (Houghton *et al.* 1996). Effects of elevated atmospheric CO_2 on terrestrial ecosystem have been extensively studied. Since 1970s much work has been reported involving in effects of ecological system, interaction in plants, insects and herbivorous animals, crop variety, biomass accumulation of plant, the ratio of below ground and above ground, metabolism and structure in plant (Lecain *et al.* 1998; Ziska *et al.* 1997; Delucia *et al.* 1997). In China the effects of elevated atmospheric CO_2 on plant growth were also studied (Bai 1996; Wei 1997; Peng *et al.* 1998). It was reported that elevated CO_2 enhanced the plant growth up to 63% (Ceulemans & Mousseau 1994). Responses of plants to elevated CO_2 were affected by plant varieties, nutrients, climate, and growth stage. Most of these studies focused on crops, while few studies related to the natural plants in temperate forests in China (Jiang 1997; Han *et al.* 2000). In this study, by using the open-top chamber to elevate CO_2 concentration, we attempted to elucidate the effects of elevated CO_2 on photosynthesis, tree growth, phytochemical components, and water use efficiency of 8 dominant tree species of the broad-leaved/Korean pine forest in temperate zone in north of China. An important objective of this research is to determine whether the responses of gas exchange in these 8 tree species in long-term controlled-environment experiments are adequate to predicting the responses of elevated CO_2 in the ecosystem and the changing tendency of their relation in future or not.

Study areas and methods

Natural condition

The study site was located at the northern slope of Changbai Mountain in Natural Reserve (42°24′N, 128°28′E) at an altitude of 736 m. The soil is mountain dark-brown forest soil. The climate is affected by monsoon and characterized by drought and windy spring, warm and rainy summer, and dry and cold winter. The mean temperature ranges from -18°C in January to 18°C in July. The average annual precipitation is 600-900 mm, with rainfall mainly from June to August. 2 271-2 503 hours are sunny and frost-free period is 100-120 d (Xu and Ding 1980).

Experimental design

The experiment was conducted at the Open Research Station of Changbai Mountain forest ecosystem, Chinese Academy of Sciences, in Erdaobaihe Town. Four open-top chambers (1.8 m in diameter steel-framed cylinders, cov-

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ered with PVC plastic film) were used. The hard pipes were installed on the bottom of each open-top chamber. Two gasbags of 5 m^3 were filled with pure CO_2 from the bottle, as the source of CO_2 for the chamber. Pure CO_2 was injected continuously into the open-top chamber through different density of pinhole on hard pipes. The open-top chambers were maintained at elevated CO_2 with the flow rate regulated to the designated treatment levels (700 μmol·mol^{-1}, two chambers and ambient 400 μmol·mol^{-1}, two chambers). Actual day-time (500-800 h) CO_2 concentration during summer averages 400 ± 38 μmol·mol^{-1} in Changbai Mountain. The CO_2 concentration at the center of each chamber was monitored with a CI-301ps Gas Exchange-analyzer (CID Inc, USA). Time for giving CO_2 into air chamber was from 6:00 a.m. to20:00 p.m. everyday. The 2-year-old seedlings of 8 tree species were germinated and grown in the nursery at Dashitou Forest Farm. The seedlings were transplanted directly in the pots in four open-top chambers on15th and 16th of April 1998. The pots, sized 28 cm in diameter and 25 cm in depth, contained 10 kg of the dark brown soil that were taken from the pine mixed broadleaved forest, carrying 37.4% of water. Ten seedlings of each tree species were planted in each chamber. The CO_2 enrichment was re-initiated when the seedlings were planted and CO_2 concentrations were maintained during day and night for whole growing season (June to October). The plants were not irrigated or fertilized.

Methods of measurement

In the growing season, the gas exchange was measured with a portable closed-loop photosynthesis system (CI-301ps CID Inc, USA). Three plants per tree species from each treatment group (fully expanded and sunlit leaves) were measured using 1/4l leaf cuvette in early August 1999. Measurements were made under saturating light (1 000-1 200 μmol·m^{-2}·s^{-1}) from the artificial cold light and at ambient temperatures, at different CO_2 levels (400 μmol·mol^{-1} and 700 μmol·mol^{-1}). The dark respiratory was measured at 0 μmol·m^{-2}·s^{-1} after 10 minutes completely darkness. The leaf was enclosed by the cuvette for 300-400 s, and leaf temperature increased by less than 2°C. Parameters calculated were Pn and Pn/E (instanteous leaf-level photosynthetic water use efficiency), a measure of carbon gained per unit water lost, where E is transpiration. Chlorophyll levels were measured with mixing solution and it was extracted in the chlorophyll extraction solution (alcohol: ethanol: sterile water = 4.5: 4.5:1) at ambient temperature in dark for 72 h. The optical density was measured with spectrophotometer. Chlorophyll content was calculated by Arnon equation (Xue *et al.* 1985).

Data analysis

One-way ANOVA was used to test the effects of the elevated CO_2 on the plant growth, gas exchange and chlorophyll. Tree species were treated separately in all analyses. Analyses were carried out using the SigmaStat 2.03 procedure of SAS.

Results and analysis

Effect of high CO_2 concentration on seedling growth

After exposure to elevated CO_2, the tree growth was enhanced. Results in Fig.1 showed that there were significant differences in collar diameters between the dominant tree species of broadleaved/Korean pine forest by t-test (P<0.05). At elevated CO_2 condition, the increase of tree heights varied with species. There was no significant difference in height growth between *Pinus koraiensis* and *Picea koraiensis* (P>0.05); but there existed significant differences between the other tree species (P<0.05). At elevated CO_2 the tree heights of *Betula platyphylla*, *Acer mono* and *Populus ussuriensis* were increased by 73.86%, 34%, and 38.09%, respectively, while those of *Pinus koraiensis* and *Picea koraiensis* were increased only by 10.12% and 11.25% respectively. The collar diameter increased by 17.63% (*Pinus koraiensis)* at least and 62.82% (*Populus ussuriensis)* at most for the eight experimental species at elevated CO_2 compared with ambient CO_2.

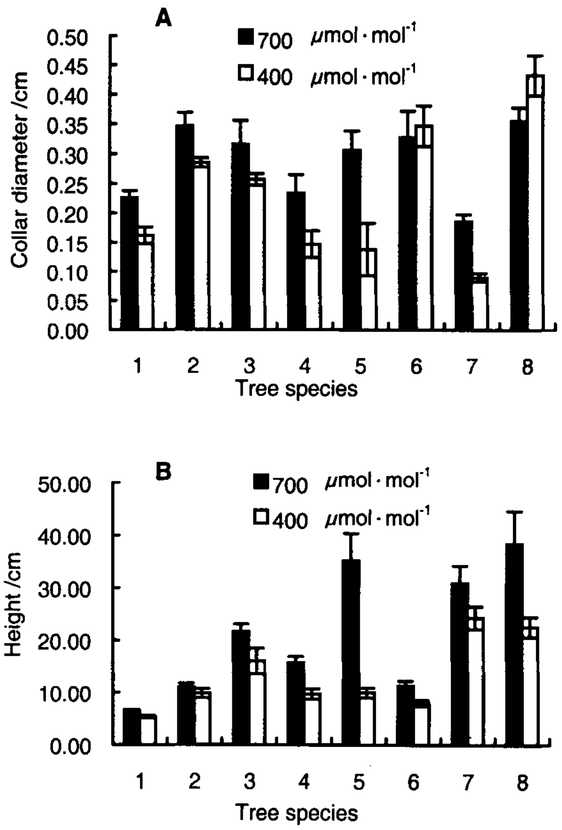

Fig. 1 Effects of elevated CO_2 concentration on growth of 8 tree species seedlings

1. *Pinus koraiensis*, 2. *Picea koraiensis*, 3. *Laxrix olgensis*, 4. *Populus ussuriensis*, 5. *Betula platyphylla*, 6. *Fraxinus manndshurica*, 7. *Tilia amurensis*, 8. *Acer mono.*

Effect of elevated CO_2 on chlorophyll content

As shown in Fig. 2, at elevated CO_2 only the species *Pinus koraiensis* had a little increase in chlorophyll content, while other 7 tree species had a little (8%) or much (30%) decrease in chlorophyll content. The chlorophyll contents of broadleaf species at elevated CO_2 followed the order of *Acer mono*< *Populus ussuriensis* <*Betula platyphylla* <*Traxinus mandshurica* < *Tilia amurensis*. There was significant difference in the chlorophyll contents of *Populus ussuriensis* and *Acer mono* between different CO_2 concentrations (Fig. 2A). In contrast, for all the species, the Chl a/b ratio was higher at elevated CO_2 than that at ambient CO_2 and the increase ranged from 9% to14%, but there was no significant difference in Chl a/b ratio between different CO_2 concentrations (Fig. 2B). This result was consistent with the studies of Delucia (1985) and Lin (1999) on cotton and four tree species of legume. Chlorophyll content and Chl a/b ratio were higher at elevated CO_2 than those at ambient CO_2, but there was no significant difference.

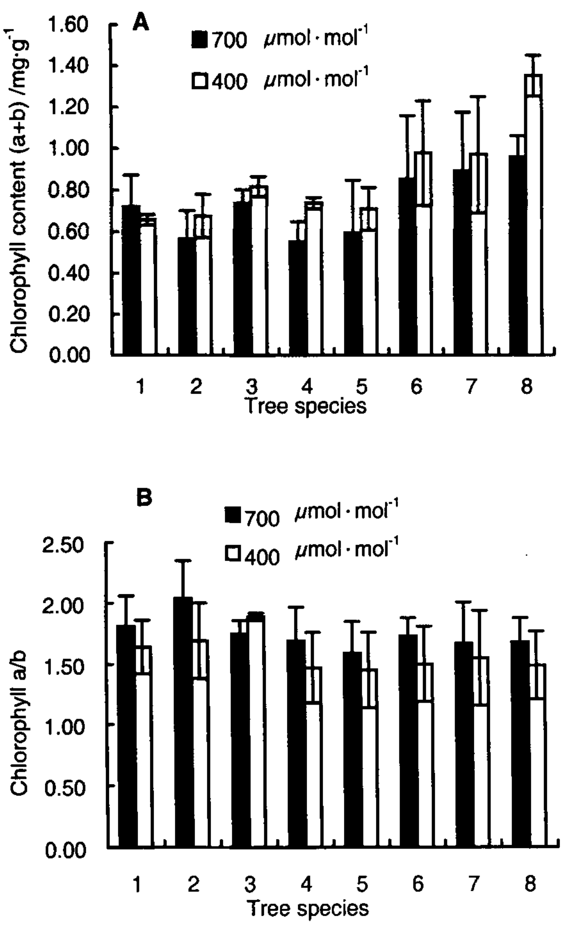

Fig. 2 Effects of CO_2 enrichment on chlorophyll content of 8 tree species

1. *Pinus koraiensis*, 2. *Picea koraiensis*, 3. *Laxrix olgensis*, 4. *Populus ussuriensis*, 5. *Betula platyphylla*, 6. *Fraxinus manndshurica*, 7. *Tilia amurensis*, 8. *Acer mono*.

Effect of elevated CO_2 on photosynthesis

Net photosynthetic rate

At different phases of the yearly growing season, the net photosynthetic rate of the seedlings at high CO_2 concentration was higher than that at ambient CO_2 and there was a significant difference (P<0.05). Meanwhile photosynthesis was determined for the 8 tree species growing at elevated CO_2 and at ambient CO_2. The results showed that the net photosynthetic rate of seedlings grown at elevated CO_2 (treatment) was higher than that of those grown at ambient CO_2 (P<0.05). The net photosynthetic rate of seedlings grown at normal CO_2 measured at ambient CO_2 was significantly higher than those at normal CO_2 (P<0.05). It indicated that elevated CO_2 could enhance the photosynthesis, and this effect was different as for different species. At ambient CO_2 (400 μmol·mol^{-1}) the average values of net photosynthetic rates of the 8 experimental species varied from 1.32 (*Pinus koraiensis*) to 11.42 (*Betula platyphylla)* μmol·m^{-2}·s^{-1} (Table 1). At elevated CO_2 the net photosynthetic rates for the 8 species increased differently and the average value ranged from 1.93 (*Pinus koraiensis)* to 15.65 (*Populus ussuriensis*) μmol·m^{-2}·s^{-1}.

Water use efficiency in leaves

Water use efficiency (WUE) was expressed as dividing the mean net photosynthetic rate by the mean transpiration rate (Table 2). The transpiration rate of the seedlings of 8 trees species grown at elevated CO_2 was lower than those at ambient CO_2. For helioskiophyte such as *Betula platyphylla*, *Pinus koraiensis*, *Acer mono* and *Picea koraiensis* the transpiration rate decreased greatly. For photophilic tree species including *Laxix olgensis* and *Populus ussuriensis* the transpiration rate reduced relatively less. A number of researches suggested that exposure to elevated CO_2 could reduce stomatal conductance, thus making the transpiration rate decrease and the net photosynthetic rate increase (e.g., Xu *et al.* 1994; Yelle *et al.* 1989). Therefore water consumption assimilating per unit carbon decreased and water use efficiency increased remarkably. In our research, the maximum of increase of WUE was found in photophilic and shade-bearing tree species such as *Acer mono* and *Tilia amurensis* and the minimum was in shade-bearing *Picea koraiensis*, which only increased by 10.01%. The results were consistent with the report of Van (1992) in spruce seedling grown at high CO_2 concentration for 5 years.

Discussions

Our findings presented some significant differences in the responses of photosynthesis and tree height as well as collar diameter of 8 tree species to long-term elevated CO_2. As CO_2 treatment prolonged, photosynthetic rates of 8 tree species were all higher at elevated CO_2 than at ambient CO_2. This indicates that high CO_2 can enhance tree growth for most of tree species.

Table 1. Effect of elevated CO_2 concentration on net photosynthesis rate of leaves of 8 tree species

Species	Measurement CO_2 level /μmol·mol^{-1}	Net photosynthesis rate/μmol·m^{-2}·s^{-1}							
		15th July		13th August		16th September		Average	
		400	700	400	700	400	700	400	700
1	400	2.27±0.37a	1.09±0.33a	1.09±0.29a	0.96±0.13a	0.59±0.58a	0.39±0.19a	1.32±0.23	0.81±0.30
	700	4.18±0.72b	2.67±0.40b	2.41±0.39b	1.59±0.28b	1.99±0.36b	1.52±0.61b	2.86±0.55	1.93±0.64
2	400	2.60±0.49a	1.16±0.46a	5.61±1.21a	1.86±0.62a	0.23±0.12a	0.26±0.13a	2.81±2.10	1.09±0.82
	700	4.05±0.98b	3.51±1.78b	8.33±1.1b	5.14±0.84b	0.85±0.56b	3.29±1.01b	4.41±3.06	2.98±2.33
3	400	3.27±0.68a	3.75±1.28a	0.64±0.31a	0.49±0.29a	0.38±0.13a	-3.45±0.89a	1.43±1.30	0.26±3.60
	700	3.75±1.28 b	5.18±1.20b	1.29±0.49b	1.01±0.42b	0.75±0.35b	0.89±0.31b	2.22±1.70	2.36±2.44
4	400	12.05±0.96a	10.22±1.26a	11.55±1.78a	12.48±2.6a	10.64±1.14a	4.02±1.17a	11.42±0.58	12.32±2.33
	700	20.82±2.16b	16.68±1.43b	19.38±1.67b	20.45±1.74b	3.99±2.73b	9.82±1.53b	18.06±2.94	15.65±4.40
5	400	7.02±1.55a	8.74±0.75a	6.17±1.43a	5.74±1.62a	9.01±1.25a	6.62±1.30a	7.40±1.19	7.03±1.54
	700	11.17±1.14b	13.41±1.16b	11.60±1.67b	8.16±1.74b	10.91±1.57a	12.72±3.00b	11.23±0.28	1.43±2.85
6	400	3.32±1.18a	4.24±1.41a	7.43±1.58a	5.81±1.82a	3.18±1.86a	1.81±1.00a	4.64±1.97	9.45±4.22
	700	4.68±0.62b	12.87±3.93b	15.27±2.55b	11.98±1.21b	4.82±1.84a	3.51±1.18b	8.26±4.94	9.45±4.21
7	400	1.89±0.12a	2.80±0.48a	4.85±0.97a	6.53±1.67a	3.51±1.36a	1.77±0.88a	3.42±1.21	8.22±3.36
	700	5.30±0.89b	8.40±1.07b	10.40±1.86b	12.24±1.28b	6.21±1.34b	4.02±1.17b	7.30±2.22	8.20±3.35
8	400	0.78±0.17a	6.15±0.89a	3.59±1.03a	4.20±1.08a	3.10±0.92a	4.14±1.28a	2.49±1.23	5.36±1.89
	700	3.37±1.01b	12.68±2.23b	10.72±1.83b	6.75±2.27b	8.43±1.37b	6.65±1.81b	7.51±3.07	8.69±2.82

Note: Values with the same letters (a, b) are not significantly different at P>0.05

Species: 1. *Pinus koraiensis*, 2. *Picea koraiensis*, 3. *Laxrix olgensis*, 4. *Populus ussuriensis*, 5. *Betula platyphylla*, 6. *Fraxinus manndshurica*, 7. *Tilia amurensis*, 8. *Acer mono*.

Table 2. Effect of elevated CO_2 concentration on transpiration rate and water use efficiency of 8 tree species

Species	Treatment CO_2 level /μmol·mol^{-1}	Transpiration rate /mmol^{-1}·m^{-2}·s^{-1}	Water use efficiency (WUE) /μmol CO_2 ·mmol^{-1} H_2O	Rate /%
Pinus koraiensis	400	0.235±0.068a	5.617±0.448a	100.00
	700	0.183±0.045a	10.540±1.707b	187.64
Picea koraiensis	400	0.557±0.164a	5.046±1.640a	100.00
	700	0.464±0.347a	5.551±1.322a	110.01
Laxrix olgensis	400	0.171±0.671a	8.389±1.823a	100.00
	700	0.170±0.472a	13.836±1.321b	164.93
Populus ussuriensis	400	1.928±0.304a	6.118±1.267a	100.00
	700	1.045±0.374a	8.849±1.334	144.64
Betula platyphylla	400	1.398±0.652a	6.984±1.981a	100.00
	700	1.045±0.374a	11.693±2.123b	167.43
Fraxinus manndshurica	400	0.949±0.475a	6.110±0.890a	100.00
	700	0.882±0.217a	12.167±3.047b	199.13
Tilia amurensis	400	0.588±0.159a	6.098±0.648a	100.00
	700	0.649±0.312a	14.980±3.652b	245.65
Acer mono	400	0.531±0.147a	5.357±0.219a	100.00
	700	0.431±0.117a	19.893±0.947b	371.34

Note: Values with the same letters (a, b) are not significantly different at P>0.05.

During whole growing season the photosynthetic rates of five broadleaf tree species except *Populus ussuriensis*, were higher at the beginning of elevated CO_2 (in July) than that at ambient CO_2 measuring at high CO_2 concentration. Photosynthetic rate was also higher at elevated CO_2 measured at normal CO_2 than those at ambient CO_2. In August elevated CO_2 still had a short-term enhancing effect on photosynthetic rate *of Tilia amurensis,* and in September the photosynthetic rates of all 6 broad-leaf tree species at high CO_2 concentration measured at normal CO_2 level were lower than those at normal CO_2 level. It represents the acclimation of photosynthesis to high CO_2 concentration (Gunderson *et al.* 1994; Genthon *et al.* 1987; Sanders *et al.* 1991; Xu 1994; Lin 1998). It was demonstrated that phenomenon photosynthetic acclimation in *Pinus koraiensis* and *Picea koraiensis* to elevated CO_2 in July was irreversible. Maybe it was due to physiological and morphological change by long-term elevated CO_2 treatment. With leaves of broad-leaf tree species expanding, the effect of elevated CO_2 on photosynthesis enhancement gradually declined.

Numerous studies have shown that after long-term exposure to CO_2 the chlorophyll content of plants decreased, the Chl a/b ratio decreased or did not change (Liang *et al.* 1997). In our study the chlorophyll contents of all 5 broadleaf tree species were higher at elevated CO_2 than that at ambient CO_2. The Chl a/b ratio was higher at elevated CO_2 than that at ambient CO_2. The results on *Picea koraiensis* out of 3 species were consistent with that of broadleaf tree species. Both chlorophyll content and Chl a/b ratio of *Pinus koraiensis* were higher at elevated CO_2 than at ambient CO_2, contrary to that of *Larix olgensis*. Therefore, chlorophyll content is not a limiting factor for net photosynthetic rate (Garbutt *et al.* 1990), which reflect complexity of responses of dominant trees species in broadleaved/Korean pine forest in Changbai Mountain to long-term elevated CO_2.

All the experimental tree species had a decrease in stomatal conductance and mean transpiration rate and had an increase in net photosynthetic rate at elevated CO_2, which led to an increase of water use efficiency. The increase of water use efficiency at elevated CO_2 was contributed to the decrease in transpiration rate or the increase of net photosynthetic rate as well as in combination of transpiration rate and photosynthetic rate (Jiang *et al.* 1999).

The effect of photosynthetic enhancement by elevated CO_2 on 8 tree species varied with time. Different tree species had different responses in tree growth and physiology to high CO_2 concentration (Xu 1994). Broadleaf trees, such as *Betula ussuriensis*, *Populus ussuriensis* and *Tilia amurensis,* had a strong response to high CO_2 concentration, while the pine trees such as *Pinus koraiensis* and *Picea koraiensis* had a weak response, which would lead to the alteration of trees species in broadleaved/Korean pine forest in global climatic change in future. The adaptation of photosynthesis of different tree species to high CO_2 concentration was different and varied with development stages of trees. It may be also affected by other environmental factors. The conclusion from the individual experiment could not be directly applied to the complicated ecosystem, and much work need to be done at molecular level for accurately understanding the mechanism of photosynthetic adaptation to elevated CO_2.

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